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Int6**Summary**

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The int6 gene was first isolated in a screen using the mouse mammary tumor virus (MMTV) as an insertional mutagen to identify genes important for breast tumorigenesis (Marchetti et al. 1995). Insertions of MMTV into int6 lead to the production of truncated proteins; expression of these truncated proteins induces transformation (Rasmussen et al. 2001; Mayeur and Hershey 2002). Reduction in int6 expression is also frequently found in human breast tumors (Miyazaki et al. 1997; Marchetti et al. 2001; van 't Veer et al. 2002). These results suggest that Int6 plays pivotal roles in mediating breast tumor formation. At the biochemical level, the Int6 protein associates with the e-IF3 complex (thus, was independently named e-IF3e; Asano et al. 1997), which is essential for translation initiation, as well as with the 26S proteasome and the COP9-signalosome (CSN; Yahalom et al. 2001), both of which are critical for proper proteolysis. However, whether Int6 functionally interacts with these protein complexes has not been thoroughly investigated in mammalian cells. Detailed functional analyses of Int6 have been provided by studies of an Int6 ortholog, called Yin6 (yeast int6), in the fission yeast, *Schizosaccharomyces pombe*. Human and *S. pombe* Int6 proteins are over 40% identical in amino acid sequences. Gene deletion studies indicate that *S. pombe* Int6 is important for a wide range of functions that are critical for proper cell division, such as spindle dynamics, chromosome segregation, and mitotic exit (Yen and Chang 2000; Akiyoshi et al. 2001). There is no evidence yet that *S. pombe* Int6 regulates bulk translation initiation (Bandyopadhyay et al. 2000; Bandyopadhyay et al. 2002). In contrast, *S. pombe* Int6 has been shown to positively regulate proteasome functioning via the control of the transport and assembly of a proteasome subunit, Rpn5 (Yen et al. 2003). Human Int6 can fully restore the localization and assembly of Rpn5 in the *S. pombe* int6-null mutant, suggesting that human Int6 may also regulate the proteasome in human cells. Intriguingly, *S. pombe* Int6 also interacts with a Ras G protein to mediate proteasome functions (Yen et al. 2003). This raises the possibility that Int6 may interact with Ras in mammals to influence tumor formation.

PM ID	Authors	Title	Journal	Pub Date
11134033	Akiyoshi Y, Clayton J, Phan L, Yamamoto M, Hinnebusch AG, Watanabe Y, Asano K	Fission yeast homolog of murine Int-6 protein, encoded by mouse mammary tumor virus integration site, is associated with the conserved core subunits of eukaryotic translation initiation factor 3.	J Biol Chem, 276, 13	30 Mar 2001
9295280	Asano K, Merrick WC, Hershey JW	The translation initiation factor eIF3-p48 subunit is encoded by int-6, a site of frequent integration by the mouse mammary tumor virus genome.	J Biol Chem, 272, 38	19 Sep 1997
11705997	Bandyopadhyay A, Lakshmanan V, Matsumoto T, Chang EC, Maitra U	Moe1 and spInt6, the fission yeast homologues of mammalian translation initiation factor 3 subunits p66 (eIF3d) and p48 (eIF3e), respectively, are required for	J Biol Chem, 277, 3	18 Jan 2002

		stable association of eIF3 subunits.		
11071923	Bandyopadhyay A, Matsumoto T, Maltra U	Fission yeast Int6 is not essential for global translation initiation, but deletion of int6 (+) causes hypersensitivity to caffeine and affects spore formation.	Mol Biol Cell, 11, 11	Nov 2000
7853537	Marchetti A, Buttitta F, Miyazaki S, Gallahan D, Smith GH, Callahan R	Int-6, a highly conserved, widely expressed gene, is mutated by mouse mammary tumor virus in mammary preneoplasia.	J Virol, 69, 3	Mar 1995
11115556	Marchetti A, Buttitta F, Pellegrini S, Bertacca G, Callahan R	Reduced expression of INT-6/eIF3-p48 in human tumors.	Int J Oncol, 18, 1	Jan 2001
11904180	Mayeur GL, Hershey JW	Malignant transformation by the eukaryotic translation initiation factor 3 subunit p48 (eIF3e).	FEBS Lett, 514, 1	6 Mar 2002
9403073	Miyazaki S, Imatani A, Ballard L, Marchetti A, Buttitta F, Albertsen H, Nevanlinna HA, Gallahan D, Callahan R	The chromosome location of the human homolog of the mouse mammary tumor-associated gene INT6 and its status in human breast carcinomas.	Genomics, 46, 1	15 Nov 1997
11536042	Rasmussen SB, Kordon E, Callahan R, Smith GH	Evidence for the transforming activity of a truncated Int6 gene, in vitro.	Oncogene, 20, 38	30 Aug 2001
11823860	van 't Veer LJ, Dai H, van de Vijver MJ, He YD, Hart AA, Mao M, Peterse HL, van der Kooy K, Marton MJ, Witteveen AT, Schreiber GJ, Kerkhoven RM, Roberts C, Linsley PS, Bernards R, Friend SH	Gene expression profiling predicts clinical outcome of breast cancer.	Nature, 415, 6871	31 Jan 2002
11029466	Yahalom A, Kim TH, Winter E, Karniol B, von Arnim AG, Chamovitz DA	Arabidopsis eIF3e (INT-6) associates with both eIF3c and the COP9 signalosome subunit CSN7.	J Biol Chem, 276, 1	5 Jan 2001
11121040	Yen HC, Chang EC	Yin6, a fission yeast Int6 homolog, complexes with Moe1 and plays a role in chromosome segregation.	Proc Natl Acad Sci U S A, 97, 26	19 Dec 2000
12553909	Yen HC, Gordon C, Chang EC	Schizosaccharomyces pombe Int6 and Ras homologs regulate cell division and mitotic fidelity via the proteasome.	Cell, 112, 2	24 Jan 2003

Regulation of Activity

Regulation of activity is not known. See Splice Variants for the possibility of producing a truncated Int6 protein that lacks the nuclear export signal at the N terminus, affecting its localization.

Interactions with Ligands and Other Proteins

Human and *S. pombe* Int6 proteins are frequently found to associate with proteasome

subunits, and a role in the regulation of the proteasome has been reported in *S. pombe*. Both human and *S. pombe* Int6 proteins bind a proteasome subunit called Rpn5 with high specificity and regulate its nuclear import and assembly into the proteasome in *S. pombe* cells (Yen, Gordon, and Chang 2003, PM ID 12553909). When Rpn5 is absent, the proteasome is inactivated because most of its subunits are improperly assembled (Yen, Espiritu, and Chang 2003, PM ID 12783882). Human Int6 may also interact with two other proteasome subunits, Rpt4 and Rpn7, as determined by the yeast two-hybrid system (Karniol and Chamovitz 2000; Hoareau et al. 2002).

The following three human Int6-binding proteins have been isolated by yeast two-hybrid screens. The physiological significance of these interactions is unclear; however, all of these proteins either have been shown to interact with the proteasome or to contain domains that can potentially bind the proteasome.

(1) Tax is an oncoprotein carried by the human T-cell leukemia virus type I and was isolated as an Int6-binding protein by Desbois and others (1996). Tax can regulate the protein levels of I κ B α , a key transcription inhibitor of the NF κ B pathway, by controlling proteasome assembly (Hemelaar et al. 2001).

(2) Rfp (RING-finger protein) was also isolated by Desbois and others (1996). Rfp contains a RING-finger domain, thus it is a presumed E3 ligase for polyubiquitination.

(3) p56, first identified as an interferon-induced element, was also isolated as an Int6-binding protein by Guo and Sen (2000). The function of p56 is unclear except that it contains a ubiquitin-like domain (Yen and Chang 2003), which may interact with the proteasome.

In addition to proteasome subunits, Int6 also frequently co-purifies with components of the CSN (Yahalom et al. 2001; Hoareau et al. 2002; Yen and Chang 2003). The CSN is best known for its role in plants to control photomorphogenesis (Wei and Deng 2003). In animal cells and in *S. pombe*, CSNs are important for signaling and regulation of cell division and differentiation. A key biochemical function of CSN is to activate a class of ubiquitin ligase, called SCF (SCF-Cullin-F box), by promoting the removal of Nedd8, a ubiquitin-like molecule, from SCF.

Int6 also co-purifies with e-IF3, which is essential for translation initiation (Asano et al. 1997), but Int6 in *S. pombe* is not essential for bulk protein synthesis (Bandyopadhyay et al. 2000). It is possible that Int6 plays a regulatory role in mediating translation.

In *S. pombe*, Int6 binds directly to Moe1 (also known as e-IF3d; Chen et al. 1999; Yen and Chang 2000), which was found in *S. pombe* to bind the Ras G-protein effector Scd1, a guanine nucleotide exchange factor for Cdc42. Genetic data show that cells lacking either *S. pombe* int6 or moe1 or both produce the same phenotype, suggesting *S. pombe* Int6 and Moe1 are subunits of the same protein complex. Human Int6 and Moe1 also interact in *S. pombe* as well as in human cells (Yen and Chang 2000).

In *S. pombe*, the deletion of both the *ras* and *int6* genes creates a synthetic growth defect; the resulting double mutant displays massive chromosome instability and loses viability readily in the cold (Yen and Chang 2000). One of the targets regulated by both Ras and *S. pombe* Int6 is the proteasome (Yen, Gordon, and Chang 2003, PM ID 12553909). Deletion of either *ras* or *int6* only modestly weakens proteasome functions, but deletion of both genes severely weakens proteasome functions. Furthermore, the presence of a hyperactive Ras rescues proteasome defects in the *S. pombe* int6-null mutant. *S. pombe* Int6 also genetically interacts with Mal3 (Chen et al. 2000), a homolog of the EB1 family of microtubule binding proteins, and with Cut8 (Yen, Gordon, and Chang 2003, PM ID 12553909), a potential proteasome tethering protein that is conserved among fungi.

PM ID	Authors	Title	Journal	Pub Date
9295280	Asano K, Merrick WC, Hershey JW	The translation initiation factor eIF3-p48 subunit is encoded by int-6, a site of frequent integration by the mouse mammary tumor virus genome.	J Biol Chem, 272, 38	19 Sep 1997
11071923	Bandyopadhyay A, Matsumoto T, Maitra U	Fission yeast Int6 is not essential for global translation initiation, but deletion of int6(+) causes hypersensitivity to caffeine and affects spore formation.	Mol Biol Cell, 11, 11	Nov 2000

11102508	Chen CR, Chen J, Chang EC	A conserved interaction between Moe1 and Mal3 is important for proper spindle formation in <i>Schizosaccharomyces pombe</i> .	Mol Biol Cell, 11, 12	Dec 2000
9892665	Chen CR, Li YC, Chen J, Hou MC, Papadaki P, Chang EC	Moe1, a conserved protein in <i>Schizosaccharomyces pombe</i> , interacts with a Ras effector, Scd1, to affect proper spindle formation.	Proc Natl Acad Sci U S A, 96, 2	19 Jan 1999
8688078	Desbois C, Rousset R, Bantignies F, Jalinot P	Exclusion of Int-6 from PML nuclear bodies by binding to the HTLV-I Tax oncoprotein.	Science, 273, 5277	16 Aug 1996
10644362	Guo J, Sen GC	Characterization of the interaction between the interferon-induced protein P56 and the Int6 protein encoded by a locus of insertion of the mouse mammary tumor virus.	J Virol, 74, 4	Feb 2000
11602750	Hemelaar J, Bex F, Booth B, Cerundolo V, McMichael A, Daenke S	Human T-cell leukemia virus type 1 Tax protein binds to assembled nuclear proteasomes and enhances their proteolytic activity.	J Virol, 75, 22	Nov 2001
12220626	Hoareau Alves K, Bochard V, Réty S, Jalinot P	Association of the mammalian proto-oncoprotein Int-6 with the three protein complexes eIF3, COP9 signalosome and 26S proteasome.	FEBS Lett, 527, 1-3	11 Sep 2002
11019806	Karniol B, Chamovitz DA	The COP9 signalosome: from light signaling to general developmental regulation and back.	Curr Opin Plant Biol, 3, 5	Oct 2000
10504338	Morris-Desbois C, Bochard V, Reynaud C, Jalinot P	Interaction between the Ret finger protein and the Int-6 gene product and co-localisation into nuclear bodies.	J Cell Sci, 112 (Pt 19)	Oct 1999
14570571	Wei N, Deng XW	The COP9 signalosome.	Annu Rev Cell Dev Biol, 19	2003
11029466	Yahalom A, Kim TH, Winter E, Karniol B, von Arnim AG, Chamovitz DA	Arabidopsis eIF3e (INT-6) associates with both eIF3c and the COP9 signalosome subunit CSN7.	J Biol Chem, 276, 1	5 Jan 2001
12695651	Yen HC, Chang EC	INT6--a link between the proteasome and tumorigenesis.	Cell Cycle, 2, 2	2003 Mar-Apr
11121040	Yen HC, Chang EC	Yin6, a fission yeast Int6 homolog, complexes with Moe1 and plays a role in chromosome segregation.	Proc Natl Acad Sci U S A, 97, 26	19 Dec 2000
12783882	Yen HC, Espiritu C, Chang EC	Rpn5 is a conserved proteasome subunit and required for proper proteasome localization and assembly.	J Biol Chem, 278, 33	15 Aug 2003
12553909	Yen HC, Gordon C, Chang EC	<i>Schizosaccharomyces pombe</i> Int6 and Ras homologs regulate cell division and mitotic fidelity via the proteasome.	Cell, 112, 2	24 Jan 2003

Regulation of Concentration

Regulation of Int6 concentration in more complex systems has not been reported. S.

pombe Int6 appears to form a dimer with another conserved protein, Moe1. If Moe1 is absent, the protein level of *S. pombe* Int6 decreases dramatically and vice versa (Yen and Chang 2000).

PM ID	Authors	Title	Journal	Pub Date
11121040	Yen HC, Chang EC	Yin6, a fission yeast Int6 homolog, complexes with Moe1 and plays a role in chromosome segregation.	Proc Natl Acad Sci U S A, 97, 26	19 Dec 2000

Subcellular Localization

In an early study of mouse mammary epithelial cells (HC11), Int6 has been shown by immunocytochemistry to be largely cytoplasmic and to concentrate in the perinuclear area (Diella et al. 1997). This pattern of localization is consistent with the possibility that Int6 localizes in the Golgi and/or endoplasmic reticulum. In a more recent study using immunostaining (Watkins and Norbury 2004), Int6 could be readily detected in the nuclei of all the cells examined, which include H1299 (human small-cell lung carcinoma), COS7 (SV40-transformed African green monkey kidney cells), MCF-10A (human mammary epithelium), HT 1080 (fibrosarcoma), HF19 (human primary lung fibroblasts), and MRC5 (human primary lung fibroblasts) cells. The localization to the nucleus can be regulated in a cell-cycle dependent manner. Watkins and Norbury (2004) examined human fibroblasts (MRC, HF19, and HT 1080) and found that nuclear Int6 is primarily found in quiescent cells. As cells approach S phase, Int6 becomes diffusely distributed throughout the cell. Furthermore, unlike normal MRC cells, in SV40-transformed MRC5 cells, Int6 is predominantly nuclear. In *S. pombe*, its Int6 ortholog localizes to the interior of the cell and associates with reticular structures and concentrates around the nuclear envelope (Yen and Chang 2000). *S. pombe* Int6 can also shuttle in and out of the nucleus, although this is not regulated by the cell cycle and is not readily detectable unless Moe1, a conserved Int6-binding protein, is absent. That is, in the *moe1*-null mutant, *S. pombe* Int6 is readily observed in the nucleus. In conclusion, Int6 proteins shuttle in and out of the nucleus in many cell types, and it will be of great importance to determine whether different functions may be regulated by Int6 in two different compartments.

Int6 nuclear shuttling is partly mediated by a leucine-rich N-terminal nuclear export signal (NES); mutations in this NES render Int6 nuclear (Guo and Sen 2000). The C terminus of Int6 may be important for its nuclear localization as truncations in the C terminus affect its nuclear localization. Guo and Sen (2000) noted that a bipartite nuclear localization signal may be present in the C terminus, however this has not been verified experimentally.

PM ID	Authors	Title	Journal	Pub Date
9260927	Diella F, Levi G, Callahan R	Characterization of the INT6 mammary tumor gene product.	DNA Cell Biol, 16, 7	Jul 1997
10644362	Guo J, Sen GC	Characterization of the interaction between the interferon-induced protein P56 and the Int6 protein encoded by a locus of insertion of the mouse mammary tumor virus.	J Virol, 74, 4	Feb 2000
15030549	Watkins SJ, Norbury CJ	Cell cycle-related variation in subcellular localization of eIF3e/INT6 in human fibroblasts.	Cell Prolif, 37, 2	Apr 2004
11121040	Yen HC, Chang EC	Yin6, a fission yeast Int6 homolog, complexes with Moe1 and plays a role in chromosome segregation.	Proc Natl Acad Sci U S A, 97, 26	19 Dec 2000

Major Sites of Expression

In mammals, int6 is ubiquitously expressed. For example, it is found in brain, lung, heart, liver, spleen, pancreas, skeletal muscle, mammary gland, lymph node, and thymus (Desbois et al. 1996).

PM ID	Authors	Title	Journal	Pub Date
8688078	Desbois C, Rousset R, Bantignies F, Jalinot P	Exclusion of Int-6 from PML nuclear bodies by binding to the HTLV-I Tax oncoprotein.	Science, 273, 5277	16 Aug 1996

Phenotypes

MMTV insertion into mouse *int6* induces breast tumor formation, most likely by creating C-terminally truncated *Int6* proteins (Marchetti et al. 1995). Expression of these truncated proteins can transform human cells in culture, and injection of these transformed cells into nude mice can induce tumor formation (Rasmussen et al. 2001; Mayeur and Hershey 2002). (Note that truncated *Int6* proteins were not detectable by Western blots in these cells, however.) Expression of *int6* is frequently diminished in human breast tumors (Miyazaki et al. 1997; Marchetti et al. 2001; van 't Veer et al. 2002) as well as in small-cell lung tumors (Marchetti et al. 2001; Watkins and Norbury 2004). *Int6*-null cells in *Drosophila* are inviable (Miyazaki et al. 1999).

In *S. pombe*, *int6* is not an essential gene. The *S. pombe int6*-null cells, albeit viable, grow slowly in the cold, a defect that is partly a result of inefficient chromosome segregation and a delay in mitotic exit (Yen and Chang 2003; Yen et al. 2003). Deletion of *S. pombe int6* also creates a wide range of defects affecting cell morphology, transport, meiosis, microtubule stability, and spindle dynamics (Bandyopadhyay et al. 2000; Crane et al. 2000; Yen and Chang 2000; Akiyoshi et al. 2001; Matsumoto et al. 2002; Yen and Chang 2003). Expression of full-length but not C-terminally truncated human *Int6* rescues these growth defects. Some of these phenotypes can be explained by the fact that *S. pombe Int6* positively regulates the proteasome. For instance, the observed inefficient chromosome segregation and mitotic exit correlate with abnormally high levels of polyubiquitinated securin and mitotic cyclin, and the *S. pombe int6*-null mutant is hypersensitive to securin and cyclin overexpression (Yen et al. 2003).

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11134033	Akiyoshi Y, Clayton J, Phan L, Yamamoto M, Hinnebusch AG, Watanabe Y, Asano K	Fission yeast homolog of murine <i>Int-6</i> protein, encoded by mouse mammary tumor virus integration site, is associated with the conserved core subunits of eukaryotic translation initiation factor 3.	J Biol Chem, 276, 13	30 Mar 2001
11071923	Bandyopadhyay A, Matsumoto T, Maitra U	Fission yeast <i>Int6</i> is not essential for global translation initiation, but deletion of <i>int6</i> (+) causes hypersensitivity to caffeine and affects spore formation.	Mol Biol Cell, 11, 11	Nov 2000
11071922	Crane R, Craig R, Murray R, Dunand-Sauthier I, Humphrey T, Norbury C	A fission yeast homolog of <i>Int-6</i> , the mammalian oncoprotein and <i>eIF3</i> subunit, induces drug resistance when overexpressed.	Mol Biol Cell, 11, 11	Nov 2000
7853537	Marchetti A, Buttitta F, Miyazaki S, Gallahan D, Smith GH, Callahan R	<i>Int-6</i> , a highly conserved, widely expressed gene, is mutated by mouse mammary tumor virus in mammary preneoplasia.	J Virol, 69, 3	Mar 1995
11115556	Marchetti A, Buttitta F, Pellegrini S, Bertacca G, Callahan R	Reduced expression of <i>INT-6/eIF3-p48</i> in human tumors.	Int J Oncol, 18, 1	Jan 2001
12136010	Matsumoto S, Bandyopadhyay A, Kwiatkowski DJ, Maitra U, Matsumoto T	Role of the <i>Tsc1-Tsc2</i> complex in signaling and transport across the cell membrane in the fission yeast	Genetics, 161, 3	Jul 2002

		Schizosaccharomyces pombe.		
11904180	Mayeur GL, Hershey JW	Malignant transformation by the eukaryotic translation initiation factor 3 subunit p48 (eIF3e).	FEBS Lett, 514, 1	6 Mar 2002
9403073	Miyazaki S, Imatani A, Ballard L, Marchetti A, Buttitta F, Albertsen H, Nevanlinna HA, Gallahan D, Callahan R	The chromosome location of the human homolog of the mouse mammary tumor-associated gene INT6 and its status in human breast carcinomas.	Genomics, 46, 1	15 Nov 1997
10375641	Miyazaki S, Rasmussen S, Imatani A, Diella F, Sullivan DT, Callahan R	Characterization of the Drosophila ortholog of mouse eIF-3p48/INT-6.	Gene, 233, 1-2	11 Jun 1999
11536042	Rasmussen SB, Kordon E, Callahan R, Smith GH	Evidence for the transforming activity of a truncated Int6 gene, in vitro.	Oncogene, 20, 38	30 Aug 2001
11823860	van 't Veer LJ, Dai H, van de Vijver MJ, He YD, Hart AA, Mao M, Peterse HL, van der Kooy K, Marton MJ, Witteveen AT, Schreiber GJ, Kerkhoven RM, Roberts C, Linsley PS, Bernards R, Friend SH	Gene expression profiling predicts clinical outcome of breast cancer.	Nature, 415, 6871	31 Jan 2002
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12553909	Yen HC, Gordon C, Chang EC	Schizosaccharomyces pombe Int6 and Ras homologs regulate cell division and mitotic fidelity via the proteasome.	Cell, 112, 2	24 Jan 2003

Splice Variants

Although Int6 splice variants have not been identified in the cell, two smaller proteins have been synthesized in in vitro translation systems (Diella et al. 1997). This presumably occurs by starting translation at two downstream AUGs. These shorter proteins lack the presumptive N-terminal NES. Thus, if produced in the cell, it is expected that these variants would be primarily cytoplasmic.

PM ID	Authors	Title	Journal	Pub Date
9260927	Diella F, Levi G, Callahan R	Characterization of the INT6 mammary tumor gene product.	DNA Cell Biol, 16, 7	Jul 1997

Antibodies

Rabbit polyclonal antibodies have been described by Desbois and others (1996), Rasmussen and others (2001), and Watkins and Norbury (2004).

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8688078	Desbois C, Rousset R, Bantignies F, Jalinet P	Exclusion of Int-6 from PML nuclear bodies by binding to the HTLV-I Tax oncoprotein.	Science, 273, 5277	16 Aug 1996
11536042	Rasmussen SB, Kordon E, Callahan R, Smith GH	Evidence for the transforming activity of a truncated Int6 gene, in vitro.	Oncogene, 20, 38	30 Aug 2001
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